Acta Œcologica
Œcol. Plant., 1985, Vol. 6 (20), n° 1, p. 73-86.

The nutrient cycling in *Quercus rotundifolia* and *Quercus pyrenaica* ecosystems (« dehesas ») of Spain

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ABSTRACT

The principal parameters of the biogeochemical cycle were determined in a semiarid ecosystem of *Quercus rotundifolia* Lam. and *Q. pyrenaica* Willd. in the central western region of Spain.

The low density of the tree layer in these ecosystems gives rise to a pronounced spatial heterogeneity in the intensity of the cycle. The fruit production of *Q. rotundifolia* is very high and contributes to increase the relative importance of the herbivore subsystem in the food chain. The presence of a well-developed herbaceous layer has the same effect.

The activity of grazing animals contributes to a considerable decrease in the turnover time of the organic material on the soil compared with other tree ecosystems.

KEY-WORDS: Quercus rotundifolia - Quercus pyrenaica - *Litter - Throughfall - Stemflow - Turnover.*

RÉSUMÉ

Les auteurs étudient les principaux paramètres du cycle biogéochimique des écosystèmes semi-arides à *Quercus rotundifolia* Lam. et *Q. pyrenaica* Willd. formant les « dehesas » du Centre-Ouest de l'Espagne.

La faible densité en arbres de ces systèmes provoque une hétérogénéité spatiale dans la répartition quantitative des différents flux. La très forte production de fruits par *Q. rotundifolia* induit un rôle important des herbivores dans la chaîne alimentaire, rôle qui est encore accentué par l'importante strate herbacée.

Dans ces types d'écosystèmes l'on assiste à une diminution considérable du temps de renouvellement (turnover) de la matière organique sur le sol, comparativement aux autres systèmes forestiers.

MOTS-CLÉS : Quercus rotundifolia - Quercus pyrenaica - *Litière - Égouttement - Écoulement - Turnover.*

INTRODUCTION

The term "dehesa" is used in Spain to refer to a particular type of tree ecosystem of low density and wide open spaces populated by herbaceous communities. Its origin lies in the primitive mediterranean and iberoatlantic mediterranean forests which were clearfelled by the inhabitants of the peninsula until the present savannah-like situation was reached. Its maintenance in this state is also the result of the activity of man and his domestic animals, as is the case of some of the typical savannahs of the world. However, human activity is now very restricted, limited to grazing by domestic animals and periodic clearing to counteract the growth of the tree layer.

These ecosystems are thus very close to natural conditions and provide an interesting offer for field study owing to their intermediate characteristics between forest communities and grasslands. Furthermore, they are extraordinarily extensive, occupying a large part of the western half of the Iberian Peninsula. In the Province of Salamanca alone, the surface occupied by these dehesas is 539,283 ha; that is 43.71 % of the provincial territory. At present, their survival does not seem particularly endangered since the soils on which they have developed do not permit any other kind of exploitation.

The tree species most frequently found on the dehesas are some of the typical representatives of the mediterranean evergreen forests: *Quercus rotundifolia* Lam. and *Q. suber* L. However, the ecotone character (Durilignosa-Aestilignosa) of the Province of Salamanca has led to the appearance of semi-evergreen species (*Q. faginea* Lam.) or even of wholly deciduous trees (*Q. pyrenaica* Willd.) in the colder and more humid areas of the dehesa distribution zone.

In such an environment, several edaphic and phytosociological studies have been carried out to date; however, there is still a lack of measurements concerning the biogeochemical cycles and the decomposition of plant debris, as is in fact the case of a large part of mediterranean ecosystems, though some studies within the framework of the IBP (see, for example, LOSSAINT & RAPP, 1978) have begun to pay attention to these areas. The aim of the present work is to contribute to knowledge of the structure and function of these ecosystems by the quantification of the nutrient flows between some of their major components.

MATERIALS AND METHODS

One of the plots studied is situated to the West of the province of Salamanca (41° 00′ N, 2° 23′ W) at 830 m above sea level. The second, farther to the South (40° 40′ N, 2° 25′ W), has a mean altitude of 850 m. Both are populated by *Q. rotundifolia*. The third (40° 37′ N, 2° 42′ W) is at 850 m a. s. l. and is populated by *Q. pyrenaica*. The aim behind this was to cover the variation range of the parameters of the biogeochemical cycle between an evergreen species and another deciduous one. Naturally, the greater area of distribution of *Q. rotundifolia* has resulted in our paying more attention to this species.

Some of the characteristics of the stands chosen were the following: tree density ranged, according to the individual plots, between 23 and 39 trees/ha; the soil surface covered by the trees' crowns fell between 11.3 and 13.2 % of the total area. The remaining surface was covered by a pasture with a predominance in the grasses *Agrostis castellana*, *Bromus madritensis* or *Elymus caput-medusae*. Below the crowns of the trees, the predominant grasses were *Dactylis glomerata* and *Bromus mollis*.

The edaphic characteristics of the stands are summarized in table I. The first of these soils is a cambisol (according to the FAO system) on granite. The second is also a cambisol but on schists. Finally, the third is an acrisol on schists. Climate was characterized by long, cold winters and short, hot and very dry summers. Mean annual temperature ranges between 11 and 12° C for all the areas studied. Mean annual rainfall ranged around 500 mm for the area populated by *Q. rotundifolia* and around 600 mm for that occupied by *Q. pyrenaica*.

Litterfall measurements were carried out by the method of continuous trapping (MEDWECKA-KORNAS, 1971) over littertraps arranged around single trees in radial form with the tree trunk at the

TABLE I. — *Physical and chemical properties of the soil from the three stands.*

Plot	Depth	coarse sand %	fine sand %	silt %	clay %
Quercus rotundifolia I	0-10 cm	44.4	26.1	19.5	10.0
	40-50 cm	38.3	28.6	17.4	15.7
Q. rotundifolia II	0-10 cm	10.9	11.4	59.4	18.3
	40-50 cm	4.6	5.1	76.6	13.6
Q. pyrenaica	0-10 cm	8.8	39.5	35.5	16.2
	40-50 cm	13.4	40.6	18.9	27.1

Plot	Depth	pH		CaO* mg/100g	O.M. %	C %	N %**	C/N	P_2O_5* mg/100g	K_2O* mg/100g
		H_2O	ClK							
Quercus rotundifolia I	0-10 cm	4.7	3.8	37	3.47	2.01	0.164	12.2	0.83	12.50
	40-50 cm	5.1	3.9	48	1.03	0.60	0.069	8.7	1.00	8.00
Q. rotundifolia II	0-10 cm	5.5	4.2	117	5.48	3.18	0.300	10.6	0.83	23.33
	40-50 cm	5.5	4.2	130	0.52	0.30	0.055	5.4	1.00	2.50
Q. pyrenaica	0-10 cm	5.0	4.1	37	9.33	5.41	0.393	13.7	2.50	25.83
	40-50 cm	5.1	3.8	37	0.81	0.47	0.050	9.4	0.83	5.17

* available

** total

TABLE II. — *Mean annual litterfall (in g/m^2) ± 95 % confidence interval.*

Quercus rotundifolia

Distance to trunk (m)	leaves	twigs	cupules	acorns	male catkins	others	total
0.50	221.71± 39.17	125.65± 19.44	50.42± 18.19	117.23± 56.74	35.94± 13.92	59.77± 10.42	610.72±109.06
2.44	201.84± 35.45	118.71± 24.75	57.88± 22.10	138.02± 71.55	27.77± 11.03	30.48± 8.30	574.70±121.93
4.38-edge	147.39± 25.45	49.43± 8.80	43.78± 19.00	105.08± 51.42	19.61± 9.22	12.80± 3.91	378.09±102.71
6.38	66.87± 10.87	5.40± 2.22	2.72± 2.13	3.05± 4.06	7.55± 3.58	3.63± 1.86	89.22± 15.14
9.38	21.28± 6.07	1.57± 1.28	0.09± 0.17		2.67± 1.81	0.89± 0.54	26.50± 7.33
13.38	6.75± 1.90	0.10± 0.07	0.08± 0.14		0.82± 0.64	0.40± 0.23	8.15± 2.19

Quercus pyrenaica

Distance to trunk (m)	leaves	twigs	cupules	acorns	male catkins and others	total
0.50	176.01± 43.15	122.93± 34.59	18.06± 26.87	46.81± 32.09	64.66± 18.12	428.47±125.82
2.29	142.54± 28.47	101.58± 32.96	19.28± 26.68	54.44± 98.81	46.65± 11.87	364.49±137.94
4.07-edge	97.50± 21.24	43.01± 13.20	12.68± 20.05	44.54± 78.12	28.51± 7.57	226.24± 95.80
6.07	63.08± 13.56	8.65± 5.82			9.52± 4.25	81.25± 14.74
9.07	27.33± 6.98	3.31± 5.22			2.86± 2.06	33.50± 8.65
13.07	14.67± 4.77	0.49± 0.74			0.67± 0.82	15.83± 5.71

centre. It was thus possible to determine the variation in litterfall with the distance from the centre of each tree. The overall duration of control was three years.

A similar arrangement was adopted for a series of rain gauges placed to collect and measure the throughfall. A device placed around the tree trunk permitted the collection of stemflow.

Periodic sampling of herbaceous material was carried out to determine pasture production.

Chemical analyses of both solid and liquid material was performed by the usual Kjeldahl, colorimetric determination, atomic absorption spectrophotometry techniques (DUQUE, 1970; GARCÍA *et al.*, 1982). In some samples of litter from *Q. rotundifolia* and from pasture, the content in organic fractions was also determined according to the method of Van Soest (GOERING & VAN SOEST, 1970).

The turnover rate of litter from *Q. rotundifolia* on the ground was estimated according to the method described by JENNY (JENNY *et al.*, 1949; OLSON, 1963).

RESULTS AND DISCUSSION

A) *Litterfall and herbage production*

The heterogeneity in the spatial distribution of litterfall due to the isolation of the trees is shown in table II, which shows the amounts of each litter component shed as a function of the distance from the trunk. Litterfall was seen to decrease gradually as distance increased, though a sharp drop could be detected from the limit of the projection of the trees' crowns over the ground.

Below the crowns of the trees, litterfall values were perfectly comparable to those normally found in forests of the warm-temperate zone (between 240 and 810 g/m^2, according to BRAY & GORHAM, 1964). They are also comparable to the data provided for *Q. ilex* by RAPP (1969 *a*) and POLI *et al.* (1974).

One peculiar aspect of *Q. rotundifolia* ecosystems is, however, the representation of each of the kinds of litter in the total and, in particular, the relative predominance of the non-leaf component of the litter. The percentages of each litter component with respect to total production are shown in table III. The percentage of non-leaf material in *Q. rotundifolia* reaches a value of 52.13 %; much higher than the average percentages of 27-31 % reported by BRAY & GORHAM (1964). In fact, of the species mentioned by these latter authors, only *Eucalyptus diversicolor* and *Pinus radiata* show percentages of non-leaf litter greater than that of *Q. rotundifolia*.

TABLE III. — *Percentages of the components of the litterfall.*

	leaves	twigs	cupules	acorns	male catkins	other
Q. rotundifolia	47.88	13.32	3.19	19.29	6.39	4.44
Q. pyrenaica	62.25	15.62	2.91	9.77	4.92	4.52

Regarding later studies, in the literature available only data for species such as the tropical *Acacia alba* (cited in JENSEN, 1974) and *Alnus rubra* (TURNER *et al.*, 1972) reveal proportions of non-leaf litter as high as those found by us.

This pronounced production of non-leaf litter is partly related to the high proportion of twigs and branches. However, the most outstanding components are the fruits. We have found no references in the scanty bibliography relating to this aspect, with the exception of the aforementioned tropical *Acacia alba*, with a proportion of fruit as high as that found by us. This is evidently a genetic trait, since a similar species, *Q. ilex*, studied by RAPP (1969 *a*) also showed a high level of acorn production.

The percentual composition of the litter of *Q. pyrenaica* seems to be much more like that of the other tree species of the warm-temperate zone (vid. *supra*).

Another important difference between the two species is the seasonality of the litterfall. The litterfall pattern for both species is shown graphically in figure 1.

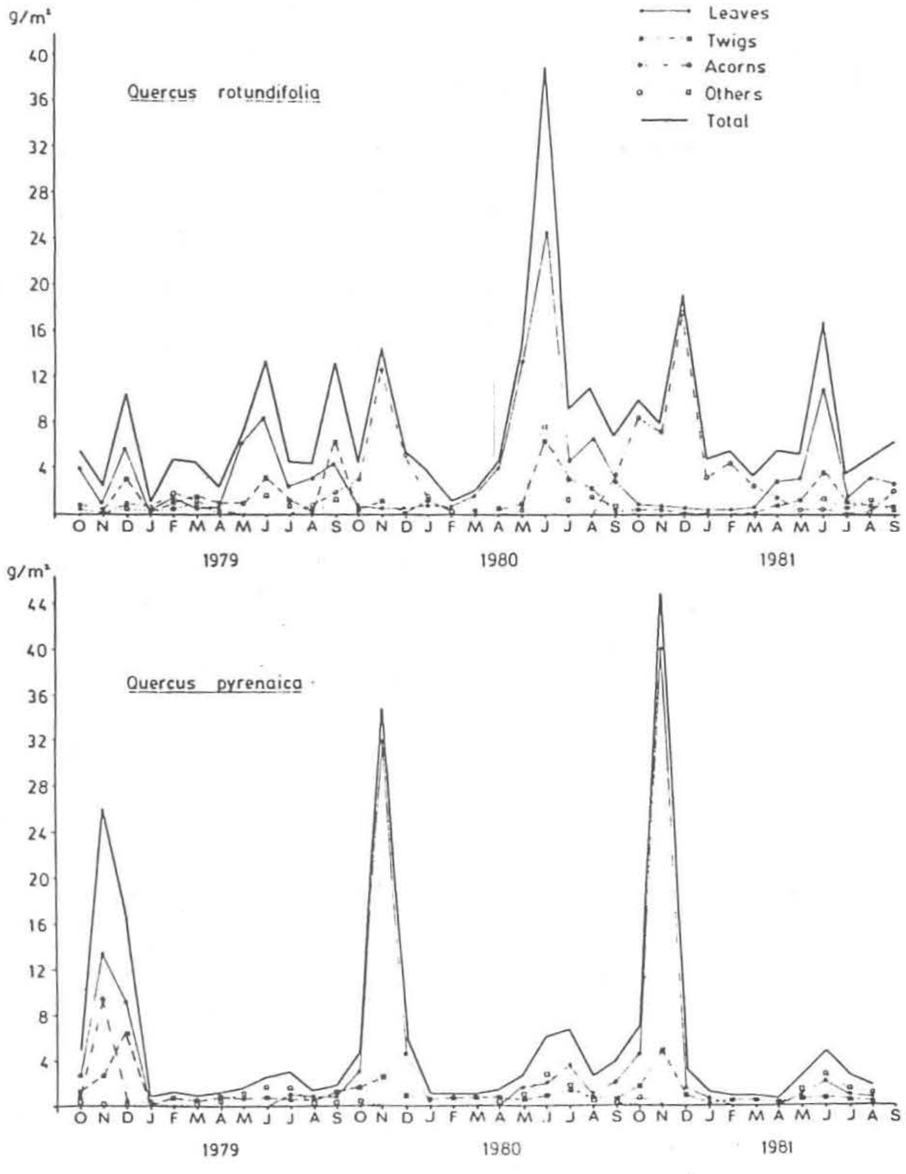

FIG. 1. — Litterfall pattern in *Quercus rotundifolia* and *Q. pyrenaica*.

Q. pyrenaica, as a typical deciduous species, exhibits a marked autumnal deposition maximum. Furthermore, the end of spring is accompanied by a secondary maximum in leaf abscission due to the action of numerous defoliating caterpillars in that period. On the contrary, *Q. rotundifolia* exhibits a more or less continuous litterfall throughout the year with two distinct maxima at the end of spring (deposition of leaves and twigs) and in mid-autumn (shedding of fruit).

The mineral composition of each of these components is shown in table IV, together with the proportions of different organic fractions and of the digestibility of the evergreen oak materials. All these values are the weighted averages of the composition of the materials shed throughout the year, which vary seasonally in their composition in a fairly uniform way.

TABLE IV. — *Chemical composition of the litterfall components.*

a) Mineral nutrients

	Q. rotundifolia	leaves	twigs	cupules	acorns	male catkins	others
%	ash	4.45	6.03	2.34	2.07	4.51	10.44
	N	0.97	0.36	0.73	0.39	1.65	1.56
	P	0.075	0.074	0.053	0.088	0.102	0.111
	K	0.231	0.238	0.415	0.297	0.228	0.375
	Ca	1.073	1.567	0.351	0.134	0.770	1.635
	Mg	0.175	0.175	0.124	0.094	0.152	0.132
ppm	Na	148.4	115.0	72.3	14.3	63.2	104.4
	Fe	123.4	103.9	38.9	17.4	163.4	413.0
	Cu	4.26	7.79	5.44	5.31	10.33	11.69
	Mn	750.2	231.5	195.6	36.9	416.0	513.9
	Zn	19.20	13.57	12.51	10.47	29.44	37.16

	Q. pyrenaica	leaves	twigs	cupules	acorns	male catkins	others
%	ash	5.70	4.15	1.00	1.43	3.72	3.92
	N	0.93	0.70	0.45	0.99	2.03	1.52
	P	0.050	0.051	0.023	0.066	0.100	0.090
	K	0.206	0.233	0.171	0.463	0.143	0.191
	Ca	1.032	1.119	0.251	0.066	0.560	0.693
	Mg	0.221	0.163	0.101	0.062	0.188	0.141
ppm	Na	134.8	136.7	12.9	1.0	58.3	35.5
	Fe	132.7	51.4	25.3	13.7	155.0	144.7
	Cu	5.32	7.42	6.26	5.66	9.79	8.93
	Mn	504.9	225.2	125.1	27.0	294.2	208.3
	Zn	16.42	23.30	5.55	7.52	25.83	24.17

b) Organic components

	Q. rotundifolia	leaves	twigs	cupules	acorns	male catkins	others
%	protein	5.96	4.70	4.41	4.32	9.63	9.06
	NDF	44.09	55.60	66.47	41.39	39.84	38.25
	CC	55.91	44.40	33.53	58.61	60.16	61.75
	ADF	40.29	55.23	52.89	30.41	34.52	35.92
	hemicellulose	3.80	0.32	13.58	10.98	5.32	2.33
	lignin	11.43	25.20	26.08	13.65	13.41	17.36
	cellulose	28.86	29.03	26.31	16.76	21.11	18.56
	DCC	41.89	30.61	19.96	44.54	46.06	47.62
	DNDF	14.40	8.39	9.12	7.01	8.72	5.51
	DMD	56.29	39.00	29.08	51.55	54.78	53.13

The organic composition of the litter shows a high incidence in its susceptibility to the processes of digestion and decomposition. The materials of organic composition most favourable for these two processes are the fruits. The digestibility values presented here appear to be excessively low owing to the inclusion of the pericarp, which is heavily lignified. However, the animals find relative ease in opening this cover to reach the endosperm, whose digestibility is high. Because of the activity of the animals, the plant nutrients contained in the fruits only reach the decomposition subsystem in small amounts, and they are recycled, in contrast, through the herbivore chain. The plant nutrients of highest concentration in the fruits with respect to the other litter components are basically nitrogen, phosphorus, potassium and copper. The acorns contain proportions of these elements ranging between 13 and 27 % of the amounts returned to the soil annually by litterfall. The other mineral elements, however, are found in very low concentrations in these reproductive organs.

The male catkins are also of an organic composition that must promote rapid processing on the soil (high cell content and a comparatively low proportion of lignin). Together with this is their richness in practically all the plant nutrients. Such organs are not consumed by herbivores, though they must undergo rapid decomposition on the soil. It is perhaps significant that it is approximately the same elements which show a special relationship to the two kinds of reproductive organs, particularly nitrogen and phosphorus. Thus, the joint contribution of both litter components tends to speed up and complicate (due to their incorporation into animals and into the herbaceous component of the ecosystem) the circulation of elements which are most important in terms of their limiting nature.

In dehesa ecosystems there are numerous open spaces between the trees. In such spaces grows a herbaceous vegetation which contributes notably to the overall production of the organic matter of the ecosystem. Table V shows the amounts of nutrients incorporated annually in the tree litterfall and in the herbage; that is, in the materials which annually are transferred to another trophic level. It should be taken in account that the ground surface covered by the crowns of the trees only represents from 11.3 to 13.2 % of the total area. Despite this, the movement of nutrients from the tree cover is enormous, and in certain cases involves more than half of the total. Apart from this, there are interesting differences between the various nutrients.

TABLE V. — *Amounts of nutrients incorporated annually in the tree litterfall and in the herbage.*

	kg/ha						g/ha				
	ash	N	P	K	Ca	Mg	Na	Fe	Cu	Mn	Zn
Q. rotundifolia											
litterfall	65.6	15.2	1.21	4.60	13.73	2.30	161.6	168.1	8.86	732	28.12
%	34.95	36.61	29.56	17.56	65.47	40.81	22.95	53.95	54.25	67.83	41.04
herbage	121.9	26.4	2.86	23.92	7.41	3.45	592.6	141.5	8.08	346	40.11
%	65.05	63.40	70.44	82.44	34.54	59.20	77.05	46.05	45.75	32.17	58.97
total	187.6	41.6	4.07	28.53	21.13	5.75	754.1	309.5	16.94	1078	68.23
Q. pyrenaica											
litterfall	79.6	17.1	0.97	4.26	14.96	3.18	199.9	175.1	10.64	629	30.78
%	41.32	42.29	27.25	20.03	58.63	47.25	23.35	36.28	54.95	60.74	48.40
herbage	113.0	23.3	2.59	17.01	10.56	3.55	656.6	307.6	8.72	406	32.81
%	58.68	57.67	72.75	79.97	41.37	52.75	76.65	63.72	45.05	39.26	51.60
total	192.5	40.5	3.55	21.27	25.52	6.74	856.6	482.7	19.36	1035	63.59

The importance of the herbaceous layer in the cycle of the different element's decreases in the order K > Na > P > N > Mg > Zn > Fe > Cu > Ca > Mn on the plots of *Q. rotundifolia*. In *Q. pyrenaica*, the sequence is similar: K > Na > P > Fe > N > Mg > Zn > Cu > Ca > Mn.

Among the essential elements, therefore, phosphorus, potassium and to a lesser extent nitrogen are cycled in relatively important amounts by the herbaceous layer. These three elements are also relatively abundant in the fruits of the trees. Another feature common to the herbaceous materials and to the fruits is their high digestibility (the herbage DMD of these communities ranges between 65 and 70 %, after GARCÍA *et al.*, 1978). Accordingly, it is again found that the most important elements are preferentially incorporated into the plant materials most available for ingestion by animals.

In any event, it seems clear that proportions of potentially edible material which is assimilable by herbivores are particularly high in dehesa ecosystems as compared with other tree ecosystems (see, for example, DUVIGNEAUD, 1968). Under such conditions it would be expected that the role of litter in nutrient regeneration should not be as predominant as usual (WHITTAKER, 1975).

Of course, the physical isolation of the trees leads to strong spatial heterogeneity in the circulation of nutrients, as happens with the deposition of organic matter (table II). The relative importance of the contribution of the tree cover decreases gradually with the distance from the centre of the tree, while the contribution of the herbaceous layer increases.

B) *Throughfall and stemflow*

Table VI shows the element loadings in rainfall, throughfall and stemflow at various locations around the tree. Naturally, the amounts which reach the ground through stemflow are small in comparison with the area covered with the trees' crowns. However, its concentration in very small surface areas around the base of the trunk means that such depositions become considerably more significant for the alteration of edaphic characters. Also appreciable from these data is that there is an additional source of spatial heterogeneity induced by the tree layer. Both the amounts of water and the amounts of nutrients received by the soil vary as a function of the distance from the centre of the tree and, of course, the figures obtained beneath the crowns of the trees are quite different from those of the areas unpopulated by trees.

The real contribution by the tree is estimated as the differences between the deposition recorded under the crown and that of the zones not reached by this part. These differences figure in table VII. It has already been mentioned that the results presented here are the means of several years' data collection on several trees in each plot. Some of the individual observations gave as a result the absence of any contribution from the tree layer and even of a retention by the crown of part of the mineral loading of atmospheric rainfall. In the averaged data, this result is only obtained for iron (the negative sign for *Q. rotundifolia* in table VII). This effect of retention of atmospheric nutrients in the trees' crowns is frequently observed in forest ecosystems (SZABÓ & CSORTOS, 1975; RAPP, 1969 *b*; PIKE, 1978). In particular, HEINRICHS & MAYER (1977) reported this same result for iron.

The input figures of nutrients by throughfall are enormously diverse for different forest ecosystems and we will therefore not compare our results with those from the available literature. However, we have noted a new and peculiar aspect in the dehesa ecosystem with respect to the contribution made by the throughfall to the total input of nutrients to the soil. Several authors (DUVIGNEAUD & DENAEYER-DE SMET, 1971; RAPP, 1971; AUSSENAC *et al.*, 1972; GOSZ *et al.*, 1976; MILLER *et al.*, 1976; COLE *et al.*, 1978) have reported that the contribution of leaching to the total deposition of nutrient elements from the tree canopies may range between 76-96 % for sodium and 0-20 % for nitrogen. Our data give the same results with respect to the relative position of the different elements in the descending series of susceptibility to leaching, though the percentages contributed by this process are much smaller, varying from 53-62 % for sodium to 0-8 % for nitrogen.

TABLE VI. — *Nutrient inputs to soil (in mg m⁻² year⁻¹) by rain, throughfall and stemflow. Average values ± 95 % confidence interval.*

a) Quercus rotundifolia

		throughfall			
		distances to trunk			
	stemflow	1.53 m	3.59 m	edge 5.62 m	rain
N	17.20±29.31	2103±2448	2595±2386	1737±1970	1898±1421
P	1.23± 2.92	113.2±117.1	145.1±138.5	73.2±50.7	62.6±61.5
K	37.4±227.3	1529± 862	1965±1057	652±603	686±442
Ca	42.3±67.9	1483±1530	1340±1765	394±189	297±275
Mg	7.00±11.25	453±273	523±314	295±149	324±273
Na	1.88±4.70	223±415	293±699	171±414	113±140
Fe	0.12±0.38	32.0±78.1	41.4±131.6	40.3±36.6	42.3±50.5
Cu	0.032±0.095	5.59±0.70	7.25±4.00	5.99±4.57	5.60±6.74
Mn	0.27±0.06	43.7±167.6	63.7±246.5	23.9±112.6	12.2±14.4

b) Quercus pyrenaica

		throughfall			
		distances to trunk			
	stemflow	1.47 m	3.41 m	edge 5.38 m	rain
N	21.31±60.36	2849±19546	3435±20647	1336±6050	2453±1510
P	1.58± 4.3[illegible]	327±2293	442±2631	50.3±21.2	113.7±59.0
K	37.9±79.7	1316±3026	1743±2722	433±350	446±276
Ca	20.3±52.1	1037±2177	1236±2712	319±1303	367±271
Mg	7.57±13.23	519±713	657±939	234±222	303±203
Na	7.31±16.15	221±1605	290±1509	162±946	125±117
Fe	0.72±1.57	45.3±345.7	57.1±325.1	47.6±276.0	45.3±41.4
Cu	0.117±0.230	9.30±69.10	11.54±55.00	7.07±41.40	3.25±7.52
Mn	0.27±0.59	35.7±259.3	46.1±243.8	18.4±106.5	17.7±16.5

TABLE VII. — *Additions of nutrients to rain by each canopy layer (mg m⁻² year⁻¹).*

	N	P	K	Ca	Mg	Na	Fe	Cu	Mn
Q. rotundifolia	125.3	33.4	773	837	95.5	126	-3.47	0.38	37.0
Q. pyrenaica	168.2	175.2	765	567	220.2	109	6.03	1.47	17.1

This greater predominance of the minerals returned to the soil in organic form should imply a clear delay in the mineral cycles with respect to what is usually observed for other ecosystems. The nutrients dissolved in rainwater decrease the turnover times of the biogenic elements on the forest floor (Gosz *et al.*, 1976) to a considerable extent. The relative scarcity in contribution of leaching in the dehesa must have the opposite effect.

C) *Estimation of the turnover of organic matter on the soil*

Table VIII shows the amounts of litter on the soil in one of the plots of *Q. rotundifolia* at the end of May. Data are shown for different distances and orientations with

TABLE VIII. — *Amounts of litter from* Q. rotundifolia *on soil at the end of May (g/m²).*

Exposure	distance to trunk (m)	leaf-litter	woody litter	total
North	1	62	470	532
"	3	54	352	406
"	5	44	199	243
"	7-edge	43	192	240
"	9	43	113	161
"	11	26	10	36
"	13	14	4	13
"	15	3	2	10
South	1	33	208	246
"	3	34	168	202
"	5	32	119	151
"	7-edge	27	71	98
"	9	20	24	44
"	11	22	14	36
"	13	16	8	24
"	15	8	3	11
East	1	36	728	764
"	3	35	488	523
"	5-edge	37	187	225
"	7	44	110	154
"	9	50	66	116
"	11	49	34	83
"	13	40	14	54
"	15	25	2	26
West	1	40	264	304
"	3	38	196	234
"	5-edge	31	90	121
"	7	21	62	83
"	9	14	40	54
"	11	11	5	17
"	13	7	3	10
"	15	5	2	7

respect to the tree because the differences associated to these two factors proved to be significant according to analysis of variance. This result is not in agreement with that obtained for the distribution of litterfall, since the differences between the orientations were not significant in this case.

This discrepancy between both groups, together with certain other anomalies which will be discussed below, must be related to the activity of grazing animals which in turn invalidates the calculation of the decay rates for each of the localizations, since the differences observed will probably not reflect the variation in the mineralizing capacity of the soil but, rather, more random factors. Consequently, it was decided to calculate the overall amount of litter on the total soil surface around each tree and then compare this mass with the fresh material added yearly by the tree over the same surface. Using this procedure, we calculated the turnover of the total organic material produced by each tree, thereby eliminating the problem of the accidental modification of the spatial distribution of the litter.

The seasonal distribution of litterfall (fig. 1) shows a marked annual maximum in the shedding of leaves and twigs which are in fact the most important materials in the construction of the reserves of organic matter above the soil, since the fruits are largely eaten by herbivores. Due to this annual maximum, the model proposed by OLSON (1963), known as the "idealized deciduous forest", was used to calculate the decay parameters. The annual loss constant is thus defined by the equation $k' = \frac{L}{L + F}$, where L = annual litterfall mass and F = mass of litter on the soil immediately before the annual litterfall peak.

Once the necessary calculations have been carried out, the estimation of the masses of litter over the soil at the end of April showed values of 16.92 g/m^2 of leaves and 46.62 g/m^2 of woody litter. In turn, the annual litterfall was 39.59 g/m^2 of leaves and 21.15 g/m^2 of twigs and branches.

Consequently, the values of k' were 0.701 for leaves, 0.312 for woody material and 0.489 for both. The average loss constants $- k = - \ln(1 - k') -$ were, respectively, 1.207, 0.374 and 0.671, implying a half-time for accumulation or decay $\left(\frac{0.693}{k}\right)$ of 0.57 years for leaves, 1.85 for twigs and branches and 1.03 for both.

The first aspect to draw our attention is the accelerated decay rate calculated. RAPP (1971) calculated a k value of 0.30 (half-time = 2.3 years) for the overall litter produced in a *Q. ilex* forest in the south of France. Other estimations of this same parameter in different temperate European and North American ecosystems (MANIL *et al.*, 1963; ROCHOW, 1974; SHARPE *et al.*, 1980) range between 0.10 and 0.80. In view of the lack of supporting data on other mediterranean type European ecosystems, it is possible that the Australian xeric communities of eucalypts resemble our environmental conditions the most. In this sense, BIRK (1979) determined a leaf decay rate of 0.68, while that of woody debris was only 0.24. Thus, the turnover rate on the soil surface of dehesa ecosystems is considerably greater than is usual in other tree ecosystems.

Other studies carried out by members of our team in the same ecosystem but using litterbags (unpublished data) allowed us to calculate a value of $k = 0.60$, which is more in agreement with the results of other authors. However, the calculation of decay rates in short-term studies using litterbags generally leads to estimations of these parameters which are greater than those obtained with the Olson's approach

(LOUSIER & PARKINSON, 1976). The main cause of this discrepancy lies in the gradual decrease of the decay rate as the material decays and loses its most labile components. This decrease in the fractional loss rate is not usually detected in short-term studies employing litterbags, thus leading to values for the accumulation of dead organic matter lower than the amounts actually found.

In contrast, our own data point to the opposite. This anomaly must also be related to the activity of grazing animals. These are likely to consume by accident part of the material deposited on the ground, and even though they do not digest more than a minimal part of this, they later return it in the faeces, after which it is subjected to new environmental conditions which are more appropriate for rapid decomposition; they may therefore be thought to carry out a similar function to that of true saprotrophs.

Thus, it is possible to observe an additional peculiarity of dehesa ecosystems. The abundance of herbivorous animals leads to a considerable increase in the turnover rate, based on unexpected decomposition rates for such sclerophyllous materials as those produced by *Q. rotundifolia*.

CONCLUSIONS

The nutrient cycling on the dehesa seems to be more complex than in other woodland ecosystems. Most of the nutrient return to soil through litterfall in other ecosystems occurs as leaf litterfall. In the communities of *Q. rotundifolia*, this fraction does not usually account for more than 50 %; the rest are found in materials of different decomposability. Some of these materials are in part consumed by herbivores and are thus not incorporated into the decomposition subsystem.

The turnover rate of the leaf litter on the soil is, furthermore, very high in the dehesa compared with other woodland ecosystems. This is due to the activity of grazing animals.

However, the proportion of different nutrients which are returned to the soil through leaching is less than in other woodland ecosystems; this should contribute to a decrease in the recycling rate of the nutrients, in part counteracting the accelerating effect of the herbivores.

The greater influence of herbivores on the nutrient cycling increases the likelihood of the export of bioelements and also the irregularity of their spatial distribution, due to the mobility of the herbivores. The elements most affected by such spatial transferences are precisely the most limiting ones (N, P and K). Suitable management of these ecosystems acquires, under such circumstances, decisive importance.

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